PREDATORY BEHAVIOR OF LARGEMOUTH BASS ON SOFT AND SPINY-RAYED FORAGE SPECIES

By

Daniel C. Hatton

A DISSERTATION PRESENTED TO THE GRADUATE COUNCIL OF
THE UNIVERSITY OF FLORIDA
IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE
DEGREE OF DOCTOR OF PHILOSOPHY

UNIVERSITY OF FLORIDA

1977

ACKNOWLEDGEMENTS

Gratitude is expressed to Dr. Merle E. Meyer for his advice and support throughout the course of this study and my graduate career. Thanks are also extended to Drs. Donald A. Dewsbury, Robert L. Isaacson, Edward F. Malagodi, and Thomas H. Patton for their critical reading of the manuscript and for sharing their knowledge with me.

A special thanks is due Gray Bass of the Fisheries Division of the Florida Game and Fish Commission and to Robert Stetler, Douglas Colle and Roger Rottman of the White Amur Research Team at the University of Florida for their invaluable aid in the collection of subjects used in this study and for their thoughtful and provocative comments on the design of the study.

A debt of gratitude is owed to Richard Kearley, Peter Spyke, Lisa Stalnaker, Rebecca Bellamy and John Heins for their help in various aspects of the study.

Appreciation is extended to Virginia Walker for her considerate attention in typing the manuscript. Finally, a special "thank you" to my wife, Nikki, for so many things, but mostly for her support, encouragement, and endurance throughout.

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By

Daniel C. Hatton

March, 1977

Chairman: Merle E. Meyer
Major Department: Psychology

The predatory behavior of captive largemouth bass, Micropterus salmoides, was observed on two species of spiny-rayed fish, bluegill, Lepomis macrochirus, and largemouth bass, and two species of soft-rayed fish, golden shiners, Notomigonous crysoleucus, and grass carp, Ctenopharyngodon idella, in three experiments. In the first experiment, the behavior of the bass and the swimming of the prey were categorized and the frequency and order of occurrence of the behavioral components were recorded. Differences were found in the susceptibility of the different species to predation and in the manner in which the predator interacted with the prey.

Susceptibility to predation was found to be consistently related to movement of the prey in the vicinity of the predator. Inhibition of movement decreased risk, while

movement, particularly rapid movement, resulted in a substantial increase in risk. Bluegill, which appeared to assume species-typical postures when motionless in the presence of a predator, were the least susceptible to predation as measured by the average sequence lenght per test trial and capture success. Grass carp had the highest risk to predation.

The presence of spiny fin rays appeared to increase the difficulty that the predator encountered in swallowing the prey. While there were no obviously different handling or capture techniques employed by the predator to capture spiny-rayed prey, it was noted that the majority of captures of such prey resulted in the prey being taken into the mouth tailfirst. The majority of captures of soft-rayed fish resulted in the prey being taken into the mouth headfirst. The difference in the position of the prey in the mouth of the predator appeared to be due more to the behavior of the prey than the behavior of the predator.

In the second experiment the bass were presented with despined bluegill. Recordings were taken on the frequency of yawns, gill flares, and headshakes that occurred after capture. Collectively, these behaviors were taken as indications that the predator was experiencing difficulty in swallowing the prey. There were significantly fewer gill flares, yawns and headshakes following capture of despined prey than after capture of spined bluegill. The difficulty the bass experienced with the despined bluegill

was significantly greater than the difficulty experienced with soft-rayed prey.

The third experiment examined the question of size selection of prey by the bass. The bass were presented with consecutive size classes of bluegill and grass carp in separate tests. The size of the first prey captured by the bass in each test was recorded. There was no evidence of size selection for either species of prey.

GENERAL INTRODUCTION

Predation can have substantial impact upon both the number and kinds of species comprising a community (Lewis, 1967; Slobotkin, 1968). Despite numerous investigations of the impact of predation, little work has been completed upon the actual behaviors involved in prey capture (Chiszer and Windell, 1973), especially for piscivorous fish. Considering the diversity of potential prey species available to most piscivorous fish, the behavioral interaction between predator and prey may be critical in determining the diet.

In the absence of behavioral data on the predator-prey interaction it is not possible to specify all of the factors that contribute to the vulnerability of a prey. Nevertheless, data from predator impact investigations indicate that there may be a limited number of variables that may account for a major portion of the variance. Lewis (1967) contends that selectivity in the predator's diet can be accounted for by variation in the vulnerability of the prey to predation.

For predators that swallow their prey intact, as do most piscivorous fish, the size of the prey relative to the size of the predator is a prime determinant of which prey are available to the predator (Lawrence, 1957). Size, how-

ever, is not a unitary variable. The size of a fish varies along four important parameters: length, depth, width and weight. The upper size limit of prey available to the predator will be set by some physical dimension of the predator, in most cases the narrowest structure leading to the esophagus (Lawrence, 1957). Consequently, depth of body may become a limiting factor before either length or width in many prey species. Weight, considered independently of other size dimensions, would not, of itself, be a physically limiting parameter but it may play a substantial role in the economic behavior of the predator insofar as weight can be considered an index to the caloric content or energy value of the prey.

An additional morphological feature of the prey that may contribute to differential selection by the predator is the spiny fin rays located in the dorsal, anal, and pelvic fins of many species of fish. Numerous species of fish have evolved specialized spines as a possible means of defence by providing aversive mechanical stimulation to the mouth of the predator that attempts to capture it (Marshall, 1966). Hoogland, Morris and Tinbergen (1957) demonstrated the utility of the specialized spines of the three-spined stickleback in defense against pike predation. Although it is not clear that defense was the selective pressure for the development of spiny fin rays, they certainly may function in that capacity given the rigidity and sharpness of the spines found in many species (Beyerle and Williams, 1968).

For visually oriented predators, movement can be a potent stimulus in the detection of prey (Walls, 1942; Marler and Hamilton, 1966). Consequently, the movement pattern of the prey in the vicinity of the predator may influence the prey's vulnerability. For the most part, movement will be the result of normal locomotion, although feeding, aggressive behaviors, and other such behavior patterns may involve very conspicuous motor patterns. Inhibition of movement in the presence of a predator may serve to lower the incidence of predation. Although varying with the predator and the situation, successful exploitation of a source of cover or utilizing cryptic coloration often depends upon the inhibition of movement. Moreover, inhibition of movement in the absence of cover or an appropriate background for effective use of cryptic coloration may also reduce the likelihood of predation, itself.

In addition to these rather general factors, there are numerous variables that probably have substantial impact on predation. Included would be such variables as reaction distance of the prey to the predator (Dill, 1974), grouping patterns (Thomas, 1974), and schooling, of both predator and the prey (Major, 1976).

The experiments described below have as their major emphasis a description of the predatory interaction of largemouth bass on various prey that differ in terms of body configuration, the presence or absence of spiny fin rays, and movement patterns.

EXPERIMENT I

Bluegill sunfish, *Lepomis macrochirus*, golden shiners, *Notomigonous crysoleucus*, largemouth bass, *Micropterus salmoides floridanus*, and grass carp, *Ctenopharyngodon idella*, were selected as prey species for largemouth bass on the basis of body configuration and availability. All of the species, except the grass carp, commonly occur in the diet of the largemouth bass (Chew, 1974). The grass carp is not indigenous to areas inhabited by the bass, but is has been introduced in some areas and does occur in the diet when available (D. Colle, personal communication).

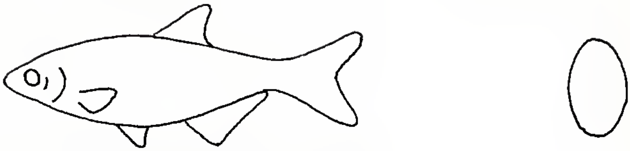
Both bluegill and largemouth bass are spiny-rayed fish, with the bluegill being relatively shorter, more laterally compressed and possessing greater body depth per unit length than the largemouth bass (see Figure 1). Shiners and grass carp, by contrast, are both soft-rayed species. The depth of body per unit length of the grass carp is less than that of the shiner, which is similar to the largemouth in that regard. Aside from the morphological differences among the prey species, it was expected from prior observation, that the fish would differ considerably in their behavior patterns.

Methods

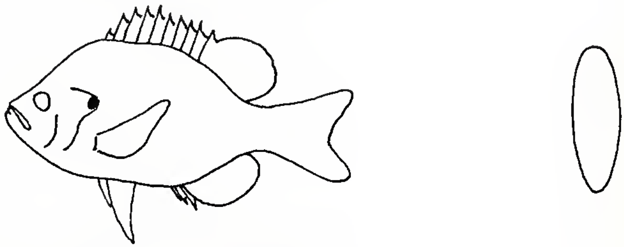
Subjects

Eight largemouth bass, obtained by electroshocking

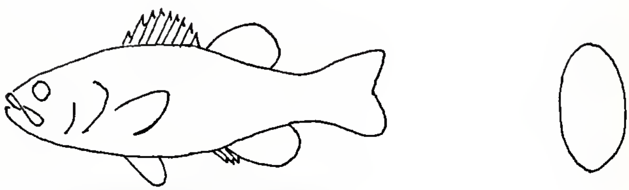
Side View Front View



Golden Shiner, *Notomigonous crysoleucus*



Bluegill sunfish, *Lepomis macrochirus*



Largemouth Bass, *Micropterus salmoides*

Grass Carp, *Ctenopharyngodon idella*

Figure 1. Body configurations of prey species.

in Newnan's Lake, Alachua County, Florida, were used as predators. Seven bass were initially used as predators in the study, however, following completion of testing on shiners and bluegill, four of the bass died, presumably as a result of disease introduced into the tank via the prey. Four additional bass were placed with the remaining three but only one survived the reorganization of the dominance hierarchy. Consequently, four bass were used in the descriptive portion for bass and grass carp. The bass ranged in size from 160 to 328 mm. These fish were maintained in a 2.4 x 1.2 x .9M plywood and fibreglass tank which was partitioned at its middle by fibreglass screening. Water in the tank was maintained at a level of approximately .6 M in depth. The water was filtered and aerated by pumping water from one end of the tank by means of a Taco model 110 pump and discharging it through a charcoal and floss filter at the opposite end. Temperature in the tank was maintained at room temperature, 21°C $\pm$ 2°C.

Bluegill, golden shiner, largemouth bass fingerlings and grass carp were utilized as prey species. The bluegill were collected as needed by seining in local lakes and ponds near Gainesville, Alachua County, Florida. The golden shiners were obtained from a local commercial supplier, while the largemouth bass fingerlings were obtained from the Welaka Natural Fish Hatchery, Welaka, Florida. Dr. Jerome

Shireman of the University of Florida contributed the grass carp for the study. The prey were maintained in a 3.05 x .46 M circular plastic wading pool and were treated with a formalin dip at 5,000 parts to 1 as well as a commercial solution of methylene blue, malachite green and acriflavin after the dip and before being introduced into the testing tank with the predator.

Procedure

Testing was conducted in one-half of the tank used to house the bass. Ten minutes prior to testing, one predator was introduced through a sliding door in the partition separating the two halves of the tank. A test consisted of a single presentation of a prey to an individual predator. The predator was allowed ten minutes in which to consume the prey. If the prey was still alive after the ten-minute period, it was removed and replaced with a different fish of the same species. The predator was allowed to eat 1 - 2% of its body weight per day in prey.

Each predator was presented with 20 prey of a variety of sizes from one species before introductions of prey from another species was initiated. The order of presentation was golden shiners, bluegill, bass and grass carp.

Prior to introduction into the testing tank each prey was weighed and measured for length and depth of body. Observations began immediately upon the introduction of the prey fish and were terminated after 10 minutes or after the prey was swallowed. In order to reduce distractions caused by the observer, the fish were viewed through a one-way glass

during testing. All data were recorded on a tape recorder and later transcribed to data cards for computer analysis.

Selected behaviors of both the predator and the prey were recorded. For the prey, swimming behavior was recorded and was broken into four distinguishable classifications:

1) Motionless - fish may be moving pectorals and riffling tail, but no movement through the water.
2) Pectoral - swimming based upon the movement of the pectoral fins.
3) Normal - whole body undulations during swimming.
4) Escape - same as 3 but much more rapid.

For predators the frequency and order of occurrence of the following behaviors were recorded:

1) Orientation - head pointed directly at the prey.
2) Approach - movement toward a motionless or pectorally swimming prey.
3) Stop - cessation of movement toward or away from the prey while remaining oriented.
4) Turn away - predator turns body away from prey.
5) Chase - rapid swimming toward a prey that is moving away.
i
6) Follow - predator maintaining a constant distance between itself and a moving prey.
7) Backpedal - pectoral swimming backwards.
8) Lunge - mouth open, gills flared, rapid thrust of body toward the prey.
9) Yawn - mouth open, gills flared, no movement of the body.

10) Rejection - prey taken into the mouth and then expelled.

11) Miss - predator lunges at prey and misses.

12) Headfirst capture - prey taken into the mouth headfirst.

13) Tailfirst capture - prey taken into the mouth tailfirst.

14) Sideways capture - prey taken into the mouth sideways.

15) Headshaking - rapid side to side movement of the head, occured after the prey was in the mouth.

16) Gill flares - gills open, mouth not open. Occurred after the prey was in the mouth.

17) Intercept - predator swims along a path that intercepts that of the swimming prey.

Results and Discussion

Description of the Predatory Interaction for all Prey

Only those behaviors that occurred while the predator was oriented toward the prey were recorded. Accordingly, all behavioral sequences recorded for the predator began with an initial orientation. For the prey, recording began with the behavior that it displayed immediately prior to orientation by the bass. The statistics presented in this section represent average conditional probabilities computed from the data for all of the fish employed in the study. Each probability presented was calculated as a per-

centage of the frequency of all behaviors following immediately upon a given conditioned behavior (Chiszer and Windell, 1973).

All trials began with the introduction of the prey into the testing tank. Following introduction of the prey, the behavioral sequence proceeded rapidly, often ending in the prey being captured within approximately 30 seconds or less. Eighty-one percent of all prey introduced were eaten within the ten-minute test trial. In many trials prey were captured more than once due to rejections and subsequent recaptures. The behavioral sequences employed by the predator will be discussed in more detail below.

Upon introduction into the testing tank the prey typically responded by swimming at normal or escape speeds ($p = .70$). In the absence of any movement by the bass toward the prey, beyond orientation, the swimming of the prey usually terminated within a few seconds of introduction by the prey becoming motionless in the tank ($p = .68$).

Orientation by the bass normally occurred immediately upon introduction of the prey into the tank ($p = .81$). An orientation was followed by either an approach, chase, intercept, lunge, follow, turnaway or yawn, depending upon the behavior of the prey and its proximity to the bass (see Table 1). If the prey was motionless or swimming pectorally subsequent to orientation there was a high probability that the bass would approach ($p = .61$). Approaches took either of two forms, the most frequent being slow, pectoral swim-

TABLE 1

Conditional probabilities for predator's behavior. Probabilities are for behaviors immediately following another behavior by the predator. S = Shiner, BL = Bluegill, B = Bass, C = Carp.

Behaviors

Behavior	Orient				Approach				Stop				Chase				Intercept			
	S	BL	B	C	S	BL	B	C	S	BL	B	C	S	BL	B	C	S	BL	B	C
Orient					64	69	54	40					13	13	31	22	04	01	01	01
Approach									71	77	60	48	01							09
Stop					56	43	44	48					02		02					
Chase									18	08	02	05								
Intercept									11			06								
Lunge																				
Miss	07				02	04			02		03		42	50	97	33				
Backpedal					04	01	25		57	44	56		02	01						
Follow									53	45	100		11	15			05			
Turnaway	70	70	67	86																
Yawn					07				07				07	04						
Headfirst																				
Tailfirst																				
Sideways																				
Gill Flare																				
Headshake																				
Reject																				
In Mouth																				

TABLE 1 (Extended)

Lunge				Miss				Backpedal				Follow				Turnaway				Yawn			
S	BL	B	C	S	BL	B	C	S	BL	B	C	S	BL	B	C	S	BL	B	C	S	BL	B	C
												-	05	02	-	04	03	02	09	04	02	-	-
16	06	11	22					01	02	06	04	θ1	02	-	-	02	04	09	13	08	07	14	04
02	01		17					16	22	24	08	02	02	-	-	14	21	22	33	03	07	07	-
40	44	48	14									01	02	-	-					06	07	-	-
22	05	08	12													04	-	-	03				
				33	57	68	36																
07	06		11					02	-	-	-	-	06	-	-	07	19	-	22	02	02	-	-
								-	-	-	-	02	-	-	-	33	46	19	67	-	01	-	-
11	03							-	03	-	-		-	-		05	18	-	-	16	15	-	-
								-	04	33	-	-	04	-	-	14	08	-	-	43	36	-	80
																				10	53	35	100'
																				100*	35	08	-
																				-			
																				-	13	07	04

TABLE 1 (Continued)

Headfirst				Tailfirst				Sideways				No Further				Gill Flare			
S	BL	B	C	S	BL	B	C	S	BL	B	C	S	BL	B	C	S	BL	B	C
10	05	-	03	19	32	50	78	04	01	-	-								
52	78	92	79	-	05	-	-	07	05	-	-								
43	14	02	18	17	26	21	45	08	-	10	05								
												30	30	33	14				
																07	24	67	-
																-	26	33	-
																08	27	13	01

TABLE 1 (Extended)

Headshake				Reject				Swim out				In mouth				Swallow			
S	BL	B	C	S	BL	B	C	S	BL	B	C	C	BL	B	C	S	BL	B	C
								01	-	-	-								
								05	04	-	33								
								01	-	-	-								
								23	13	-	33								
								02	06	-	-								
-	12	-	-	-	08	-	-					92	94	100	100				
				08	06	-	-					92	94	100	100				
				09	28	05	-					91	72	95	100				
				33	-	-	-					03	-	-	100				
10	02	-	-													80	45	65	-
				-	06	-	-									100	28	59	100
02	29	14	10													90	31	66	85

ming toward the prey interspersed with numerous stops. The other form of approach was rapid whole body swimming toward the prey.

Prey which continued swimming either normally or at escape speeds following orientation increased the probability that the bass would either chase ($p = .16$), intercept ($p = .11$), follow ($p = .02$) or lunge ($p = .02$) at it. Chases occurred most frequently ($p = .80$) to prey swimming at escape speeds away from the bass. Most intercepts, on the other hand, occurred while the prey was swimming normally ($p = .75$). Following pursuant to orientation was directed exclusively toward normally swimming prey.

Lunges which followed upon orientation occurred when the prey swam into the immediate vicinity of the bass. Similarly, most yawns following orientation were toward prey in close proximity to the bass. Turn aways were not consistently related to the behavior of prey immediately following orientation.

While an approach was the most frequently observed behavior following an orientation, a stop was the most frequently observed behavior following an approach ($p = .64$). Most of the stops occurred during the pectoral approach sequence. Typically, in the pectoral approach sequence, the bass would swim a portion of the distance between itself and the prey, stop, and then again resume its approach. As many as a dozen such approach-stop sequences may occur before the bass came to rest within a few cm of the prey.

Aside from the stop, the most frequently observed be-

havior following an approach was a lunge ($p = .14$). Lunges in this context, were directed toward motionless prey after the bass had approached to within 10 cm of the prey or closer. The lunge itself was characterized by a rapid thrust of the body toward the prey while the mouth was opened, which created a strong water current into the mouth (Nyberg, 1971).

Yawns followed approaches 8% of the time. Yawns were directed at the prey from an average distance of approximately 5 cm, and involved the bass opening its mouth and creating a local water disturbance that was directed away from the bass. No gross body movements were observed during the yawn except the opening of the mouth. The probability that the prey would respond to a yawn was .73 (see Table 2). Most of those responses were escape swimming away from the bass ($p = .75$). This can be contrasted to the .3+ probability of responding to an approach.

The most frequently occurring behavior following an approach was a stop. Likewise, the most frequent response following a stop was an approach ($p = .48$). This outcome is primarily due to the approach-stop sequences employed by the bass. A further outcome of this process is that many of the behaviors observed following a stop were part of the approach-stop sequence, as well. This is particularly true of yawns ($p = .05$) and lunges ($p = .04$) which tended to occur when the bass stopped within 10 cm of the prey following an approach and is also true of backpedals ($p = .18$)

TABLE 2

Predator behavior conditional upon prey behavior. Predator behavior immediately follows prey behavior. M = Motionless, P = Pectoral, N = Normal, E = Escape.

Prey Species

Behavior	Shiner				Bluegill				Bass				Carp			
	M	P	N	E	M	P	N	E	M	P	N	E	M	P	N	E
Orient	56	58	55	21	30	55	54	29	52	67	63	20	58	69	82	19
Approach	19	16	03		18	13	03		06	33	02		06	06		
Stop	12	12	02	04	26	08	09	04	28		04		06		02	
Backpedal	04	03	01	01	03	05	04	03	03			04	03			
Chase		01	09	25		01	04	36			10	43			02	43
Follow		02	04	07		06	15	01			06				02	
Intercept			02								10			13	04	
Turnaway	04	05	10	09	14	06	05	02	07		04		24	06	01	04
Lunge	02	01	05	02	01		04	09			02	26			01	12
Miss			02	10				05				04				08
Swim Out			06	20		06	08	08				03	03	06	04	08

which were interspersed into the approach sequence. A bass may approach, stop, then backpedal and stop, and then again approach. This type of sequence was common.

Turning away from the prey occurred with appreciable frequency ($p = .23$) following a stop, but was much more frequent following a backpedal ($p = .41$). In fact, turning away occurred at almost the same frequency as that with which a stop followed a backpedal. Turning away and stopping accounted for 90% of the responses following a backpedal.

Chases, intercepts and follows could occur only when the prey was moving. As mentioned previously, chases occurred with the greatest frequency whenever the prey was moving at escape speeds (see Table 3). Thus, chases occurred most frequently following behaviors by the predator that increased the probability of the prey making escape maneuvers. In this regard, initial introduction of the prey along with lunges, yawns and rapid approaches were the setting conditions for the majority of the escape responses by the prey.

The most frequent responses following a chase were lunges ($p = .37$) and tailfirst overswims ($p = .45$). These represent the two basic ways that a bass captures its prey. In the overswim, the bass simply swims over and engulfs the prey (Nyberg, 1971). Lunges, which were described above, occurred whenever the prey deviated from its swim path as the predator was about to overtake it. Most lunges occur-

TABLE 3

Conditional probabilities for prey behavior contingent upon immediately preceding predator behavior. PR = Probability that the prey would respond. M = Motionless, P = Pectoral, N = Normal, E = Escape.

Prey Species

Behavior	Shiner					Bluegill					Normal					Carp				
	PR	M	P	N	E	PR	M	P	N	E	PR	M	P	N	E	PR	M	P	N	E
Orient	13	42	35	13	10	12	70	10	13	06	05	40	20	40		13	63	25		12
Approach	11	08	20	30	42	22	22	13	30	35	56	11		18	70	48	14		43	43
Stop	16	24	22	24	30	13	36	38	19	07	27	25	13	38	25	40		88		12
Backpedal	17	56	11	33		12	64	29	07		16	33		67						
Chase	06	86		14		29	82	03		15	16	63			37	08	33			67
Follow	32	67	22	11		57	86	02	05	07	83	60			40					
Intercept	07	50			50															
Lunge	11			23	77	09			12	88					100	08				100
Miss	50	49	23	23	05	25	76		12	12	22	45	36	18						
Yawn	77		06	15	78	79	04	07	22	67	67			11	89	69	27	09	64	

ring in this context resulted in the predator missing the prey.

In the majority of cases intercepts were directed toward prey which were swimming normally. Here again the overswim mode of capture was the most successful, with the prey being taken head on and it was also the most frequent outcome of an intercept ($p = .75$). As with chases, lunges occurred whenever the prey veered away from the predator immediately before contact.

The majority of follows were of normally swimming prey ($p - .57$), and were usually terminated by the predator stopping ($p = .50$). Following could be accomplished by the predator swimming pectorally, normally, at chase speed or by backpedalling. The defining characteristic was a constant position between the predator and the prey. The high incidence of stopping pursuant to a follow was due to the tendency of the prey to become motionless when followed ($p = .71$). Similarly, chases were terminated first by the prey stopping and then the predator stopping ($p = .66$) (provided that the prey was not captured by the bass beforehand).

There were several responses that commonly followed captures. Gill flares, head shakes and yawns prior to swallowing or rejecting the prey occurred frequently. These responses will be discussed in more detail below.

Prey Species Differences

There were a number of differences in the behavioral interactions observed among the different species of prey

and the predator. One measure of these differences is in the average number of behaviors engaged in prior to the termination of a test. The mean values for sequence length were 26.1 for the bluegill, 17.2 for shiners, 12.1 for the bass and 9.3 for grass carp. The analysis of variance for k independent groups (Freund, 1967) showed a significant difference among the groups ($F=10.43$, $df=3,429$, $p < .05$). Duncan's multiple comparison procedure revealed that there were significantly more behaviors employed in the bluegill-bass interaction than to the remaining species ($k=6.52$, $p < .05$). The number of behaviors in the shiner-bass interaction was significantly greater than the carp-bass interaction ($k=6.86$, $p < .05$) but not significantly different than the bass-bass interaction. The bass and carp did not differ significantly from one another in sequence length per test trial.

Mode of Capture

All captures occurred as a consequence of a chase, lunge or intercept. Table 4 lists the relative frequency of occurrance of each of the different modes of capture for each species along with the outcome of the attempts. Except for shiners, intercepts were the most efficient means of capturing prey whereas chases were the more frequent method attempted. For shiners, the lunge was both the most efficient and more frequently occurring method of capture.

Ninety-five percent of the captures subsequent to intercept resulted in the prey being taken into the mouth headfirst whereas 85% of the captures following a chase

TABLE 4

Attempted captures/successful captures.
A = Attempt, H = Headfirst, T = Tailfirst, S = Sideways.
Prey Species

Behavior	Shiner				Bluegill				Bass				Carp			
	A	H	T	S	A	H	T	S	A	H	T	S	A	H	T	S
Intercept	32	16	0	2	21	16	1	2	15	12	1	0	38	27	0	0
Chase	100	10	19	4	138	6	32	1	103	0	43	0	41	1	28	0
Lunge	127	5	20	5	116	15	26	3	66	1	13	0	25	4	10	1

ended with the prey in the mouth tailfirst. There are no significant differences among the species in this respect. Lunges resulted in tailfirst captures most often in all species but shiners where the majority of lunges resulted in headfirst captures. This result appears to be due to significantly more lunges ($p < .05$) made to shiners swimming pectorally or normally than to the other species where most of the lunges were made to prey moving at escape speed.

Efficiency

In part, the sequence length reflects the efficiency of the predator in capturing the prey. A more accurate indication of the efficiency of capture is given by the ratio of captures to attempted captures presented in Table 4.

The highest efficiency was achieved in the carp-bass interaction where the success rate for attempted captures was 67%. Z-tests of proportion (Fruend, 1967) showed this value to be significantly different from the values obtained for the other species ($p < .05$).[1] The 49% success rate for the shiner-bass interaction differs from both the bass-bass and bass-bluegill interactions ($p < .05$), while the bass-bass and bass-bluegill interactions did not differ ($p > .05$).

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[1]All values for Z-tests in this and subsequent sections are presented in Appendix 1.

Movement

The capture success data are somewhat surprising in view of the data on sequence length, particularly in regard to the bass, bluegill and shiner data. One reason for the disparity between the sequence lengths and capture success is the risk incurred by the prey as a function of movement. Table 5 presents the number of responses made by each species in each movement category and the number of captures that occurred while the prey was engaged in that behavior.

As can be seen from Table 5, most of the captures occurred while the prey were moving normally or at escape speed. For grass carp, 93% of the captures occurred while the fish was swimming normally or escaping with 47% of such responses by the carp resulting in capture. At the same time, 63% of the responses made by the carp were in the normal or escape category. These values are very similar to the values obtained for bass fingerlings where 97% of the captures occurred during normal or escape swimming while 62% of such responses resulted in capture. Sixty percent of the responses made by the bass were in the normal and escape swimming categories. The values for the carp and the bass did not differ significantly from one another with regard to frequency of normal and escape swimming ($p > .05$) but did differ in risk with bass having a significantly higher risk while swimming at normal and escape speeds ($p < .05$).

Bluegills made the smallest number of normal and escape responses for a 40% ratio and had the lowest capture ratio

TABLE 5

Number of responses by each prey in each of the swimming categories and number of captures during each category. M = Motionless, N = Normal, P = Pectoral, E = Escape.

Prey Species

Behavior	Shiner				Bluegill				Bass				Carp			
	M	N	P	E	M	N	P	E	M	N	P	E	M	N	P	E
Responses	140	142	95	122	323	176	184	169	76	59	9	71	55	106	22	25
Captures	18	53	24	32	19	39	5	44	2	31	0	50	3	47	2	15

for the responses ($p = .23$). Shiners made significantly more normal and escape responses ($p = .56$) with a significantly higher risk to the fish ($p < .05$).

Motionless

All of the species had a relatively low risk while motionless or swimming pectorally as can be seen from Table 5. Shiners had the highest risk while motionless ($p = .13$) which was significantly higher than all other prey ($p < .05$) except grass carp ($p > .05$). The other species did not differ significantly from one another ($p > .05$). There were differences in the positions in the tank that the prey typically assumed when motionless that may have contributed to the differential risk while motionless.

Bluegill tended to become motionless at the sides and in the corners of the tank with the side of the fish pressed closely against the wall. Often the fish would be oriented perpendicular to the normal swimming position with either the head or the tail in the up position. At other times they would rest against a surface with the body tilted 90° from the vertical axis with the dorsal or ventral surface against the wall.

Shiners also tended to become motionless near the sides and in the corners of the tank, but the posture of the fish was normal in the sense that the body was in the normal swimming posture. Bass fingerlings usually were motionless on the bottom of the tank irrespective of position relative to the sides of the tank. Carp did not appear to become

motionless in any one position in the tank any more than any other position.

Both the carp and the bass were significantly more responsive to approaches by the predator when motionless than either bluegill or shiners ($p < .05$) but did not differ beteeeen themselves ($p > .05$). Shiners were significantly less responsive than bluegill ($p < .05$). As a consequence of the responsiveness of the bass and carp to the approach of the predator, the predator did not often approach close enough to these species to lunge at them while they were motionless. While shiners were the least responsive to approaches by the predator when motionless, significantly more lunges were directed toward the shiners when motionless than to bluegills with a greater success ratio ($p = .88$ vs $p = .66$, $p < .05$).

<u>Yawns</u>

Yawning occurred in three contexts. Bass were observed to yawn in the absence of prey, when the bass was within 10 cm and oriented to the prey, and after the prey had been taken into the mouth. Yawning in the absence of a prey was not recorded. The frequency of occurrence of yawns in the other situations are presented in Table 6.

There were significantly more yawns ($p < .05$) directed at bluegill and shiners before capture than at carp or bass, the majority of which were directed at motionless and pectorally swimming prey. The outcome of this type of yawn was usually movement by the prey at normal or escape speed

TABLE 6

Number of yawns occurring before and after capture.

	Prey Species			
	Shiner	Bluegill	Bass	Carp
Before capture	64	98	10	2
After capture	2	46	13	4

(p = .61). It appeared that this behavior served to induce movement by the prey which, in turn, increased the risk to the prey.

Difficulty

Yawning that occurred after the prey was in the predator's mouth was often in conjunction with headshaking and gillflaring. Collectively these behaviors were taken as indications that the predator was experiencing difficulty in swallowing prey. The frequency of occurrence of these behaviors are presented in Table 7.

Any or all of these responses could occur following any given capture and each of the behaviors could be repeated more than once following a capture. Significantly more of the responses were shown for the two spiny-rayed species than to the soft-rayed species ($P < .05$) which did not differ from one another ($p > .05$).

Rejections

Rejections were often associated with the responses that indicated difficulty in swallowing but not always. There were 15 rejections of shiners, 24 of bluegill, 3 of bass and no carp rejections. All of the rejections of shiners occurred in the absence of any of the responses indicating difficulty in swallowing. Seventy-three percent of the rejections of bluegill followed tailfirst captures as did all of the rejections of bass. Only 27% of the shiner rejections followed a tailfirst capture. There were significantly more rejections of bluegill than of the re-

TABLE 7

Number of gill flares, yawns and headshakes following captures.

	Prey Species			
Behavior	Shiners	Bluegill	Bass	Carp
Gill Flare	8	42	17	1
Yawn	2	46	13	4
Headshake	1	35	12	7
Capture	127	107	70	81

maining species ($p < .05$) which did not differ among themselves ($p > .05$).

Size Differences

Werner (1974) has suggested that the optimal prey size for a piscivorous predator is 0.59 times the gape width of the predator's mouth to body depth, based on handling time from capture to swallowing. Since Werner established this figure with bluegill and green sunfish as predators on inanimate prey, its generality to the present situation is debatable. Nevertheless, it does provide a point of departure for examining the effect of body depth on the behavior of the bass. Accordingly, the data were sorted into two groups for each species based on whether or not the body depth exceeded 0.59 times the gape width of the predator involved. The data were then analyzed in the same manner as employed in the previous section.

The results were that only seven of the 80 grass carp presented to the bass exceeded the 0.59 cutoff. In contrast, 109 of the 132 bluegill presented were greater than 0.59 the gape width. The figures for shiners and bass showed similar trends in group size with 40 of the 140 shiners greater than 0.59 and 14 of the 80 bass greater than 0.59. Due to the disparity among the group sizes, an analysis of variance was not performed on the sequence lengths. The mean sequence lengths are presented in Table 8.

With the exception of the data on carp, the means for the groups exceeding 0.59 were consistently greater than the group means for the smaller fish. The relative ordering of

TABLE 8

Mean sequence length for prey smaller and larger than 0.59 times the gape width of the predator's mouth.

Gape width of bass	Prey species: Shiner	Bluegill	Bass	Carp
Below 0.59	12.03	18.5	9.55	9.6
Above 0.59	28.23	29.0	24.42	6.3

the means among the species is the same as observed in the previous section.

Bluegill

While the mean sequence lengths for the two groups of bluegill indicated a greater efficiency on the part of the predator in capturing the smaller fish, there were no significant differences in the capture/success data for the two groups ($p > .05$). These data are presented in Table 9.

There were, however, a significantly greater number of attempted captures of smaller fish ($p < .05$). For the most part, the differences in sequence length between the two groups appeared to be due to a greater number of behaviors directed toward the larger prey. Most of the additional behaviors appeared to be attempts on the part of the predator to place itself in a position to capture the prey. Specifically, there were significantly more approaches, stops, follows and yawns before capture for the larger fish ($p < .05$). There were more large prey taken headfirst and significantly fewer large prey taken tailfirst ($p < .05$).

Although there were significantly more yawns following captures of large prey ($p < .05$), there were no differences between the two groups among the other behaviors, indicating difficulty in swallowing ($p > .05$).

Bass

The data for bass fingerlings show that the capture/success ratio was significantly higher for the small fish than for the larger fish ($p < .05$); while attempted captures

TABLE 9

Number of attempted captures and the position of the prey in the mouth following capture for bluegill above and below 0.59 times the gape width of the predator's mouth.

		Attempt	Head	Tail	Side
	Intercept	16	12	0	2
Above 0.59	Lunge	88	13	19	2
	Chase	111	5	23	1
	Intercept	5	4	1	0
Below 0.59	Lunge	28	2	7	1
	Chase	27	1	9	0

were similar for both groups ($p > .05$). These data are presented in Table 10.

There was no difference between the swimming behavior of the two groups ($p > .05$) and only during escape swimming did the small fish incur a higher risk than the large-er fish ($p < .05$). Yawning occurred more frequently before captures in the larger group than in the smaller group as did the number of approach-stop sequences ($p < .05$). The predators seemed to have some of the same problems with larger bass fingerlings that they experienced with large bluegill. While the greater number of misses of larger prey may be accounted for by the fact that a larger fish is a stronger swimmer and therefore is more capable of eluging the predator, the approach-stop sequence and yawning suggest that the predator engages in more behaviors preparatory to an attempted capture. Yawning after capture was similar in both groups as were gill flaring and rejections ($p > .05$) but more headshaking was evident after capturing larger fish ($p < .05$).

Shiner

The data for shiners were very similar to those for bass. There was a significant difference in the capture/success ratio between the two groups ($p < .05$), with more of the smaller prey being captured per attempt than the larger prey (see Table 11). Although there were no differences in the number of attempted captures between the two groups ($p > .05$), there were significantly more chases

TABLE 10

Number of attempted captures and the position of the prey in the mouth following capture for bass above and below 0.59 times the gape width of the predator's mouth.

		Attempt	Head	Tail	Side
	Intercept	5	3	0	0
Above 0.59	Lunge	21	0	1	0
	Chase	43	0	9	0
	Intercept	10	9	1	0
Below 0.59	Lunge	45	1	12	0
	Chase	60	0	34	0

TABLE 11

Number of attempted captures and the position of the prey in the mouth following capture for shiners above and below 0.59 times the gape width of the predator's mouth.

		Attempt	Head	Tail	Side
	Intercept	17	6	0	1
Above 0.59	Lunge	48	11	3	3
	Chase	56	2	7	3
Below 0.59	Intercept	15	10	0	1
	Lunge	79	39	17	2
	Chase	44	8	12	1

and fewer lunges directed toward the larger prey ($p < .05$).

There were differences in the swimming behavior of the prey with the larger prey becoming motionless more often than the smaller prey ($p < .05$), while the smaller prey engaged in more normal swimming ($p < .05$). In all swimming modes, the smaller prey had a higher risk of predation than the larger prey ($p < .05$).

As with the larger bass fingerlings, the differences between the two groups of shiners appeared to be due to the ability of the larger fish to elude the predator. However, there were no significant differences in the numbers of approach-stop sequences although there were significantly more yawns before capture for the larger group ($p < .05$).

<u>Carp</u>

There were essentially no differences in the data for the two groups of grass carp.

EXPERIMENT II

The descriptive data from Experiment I suggest that the predators experienced more difficulty in swallowing spiny-rayed prey than with soft-rayed species. This was indicated by the greater number of yawns, gill flares, and headshakes following captures of spiny-rayed prey. To test the hypothesis that the spines themselves were the source of the difficulty, the predators were presented with bluegill which had had the spines removed from the dorsal, anal, and pelvic fins.

Methods

Subjects

The predators were the same as those used in the previous study. Four additional bass, housed and tested in individual 68-liter aquaria, were added to the study. These bass were obtained in the same manner as the bass for Experiment I and were maintained in the laboratory for three months prior to testing. The bluegill were collected and maintained as in Experiment I.

Procedure

The procedure was similar to that used in Experiment I, except that the spiny portions of the fin rays were removed with surgical scissors after the prey had been weighed and measured. Swimming behavior did not appear to be substan-

tially affected by the removal of the spines.

The control data were those on intact bluegill from Experiment I. Since the intact fish had not been traumatized, only mode of capture, position of the prey in the mouth as well as yawns, gill flares, headshakes and rejections following capture were recorded for the despined prey. Recordings were made as in Experiment I.

Results and Discussion

There were significantly fewer gill flares, yawns, and headshakes following the capture of despined bluegill than after the capture of spined bluegill ($p < .05$). There were also significant differences in the mode of capture, intercepts, lunges, and chases, employed by the predator for the two groups of fish ($p < .05$). However, mode of capture did not appear to have a significant effect upon the difficulty the predator encountered in swallowing the prey (see Table 12) although there were significantly more rejections of spined bluegill that were taken into the mouth tailfirst than those taken headfirst ($p < .05$).

More of the attempted captures of despined bluegill were intercepts and lunges ($p < .05$), while there were fewer chases ($p < .05$). As a consequence, more of the despined bluegill were taken into the mouth tailfirst ($p < .05$). The distribution of yawns, gill flares and headshakes as a function of the position of the prey in the predator's mouth showed that significantly more headshaking ($p < .05$) occurred after a tailfirst captures than after head-on cap-

TABLE 12

Behavior that occurred after capture of spined and de-spined bluegill.

		Behavior				
		Gill Flare	Yawn	Head-shakes	Reject	Capture
Spined	Headfirst	22	18	7	1	37
	Tailfirst	20	28	28	14	59
	Total	42	46	35	15	96
De-spined	Headfirst	8	5	2	7	48
	Tailfirst	7	4	11	4	34
	Total	15	9	13	11	82

tures in both spined and de-spined fish. In the spined group, significantly more gill flares occurred after headfirst captures than after tailfirst ($p < .05$) captures, with yawns being more evenly distributed between head and tailfirst captures ($p > .05$). The de-spined group showed no differences for position in the mouth and yawns or gill flares ($p > .05$).

Presumably these behaviors are related to the positioning of the prey in the mouth preparatory to swallowing and it may well be that each of the behaviors is uniquely related to this function. However, in the majority of cases, since the prey could not be viewed by the observer, the function or result of each of these behaviors could not be differentiated. Nevertheless, it remains the case that there existed differences related to both the position of the prey in the mouth and the behavior of the predator following capture.

On the few occasions in which the prey could be observed in the mouth of the predator it appeared to the observer that more headshaking occurred when the prey was obviously stuck in the mouth. According to Lawrence (1957), who took X-rays of the position of the prey in the mouth prior to swallowing, the prey is turned 90° to the vertical axis before swallowing. On the few occasions that the prey was observed to be positioned in the mouth on the vertical axis and the mouth was propped open, headshaking was employed by the predator to dislodge it.

EXPERIMENT III

Size selection of prey by a predator has received considerable theoretical treatment in the literature (Ivlev, 1961; Schoener, 1969; Werner, 1974) with most authors agreeing that there is an optimal size of prey for a given sized predator. There have been two investigations of size selection by largemouth bass; both obtained equivocal results. Tarrant (1960) found a positive correlation between prey size and predator size using green sunfish as prey, while Wright (1970) reported no evidence of size selection of gizzard shad. It should be noted that, amongst other differences, Tarrant employed spiny-rayed prey and that Wright worked with soft-rayed prey.

The data from Experiment I indicate that the predator experiences greater difficulty in capturing larger prey than smaller as evidenced by longer sequence lengths and a greater number of unsuccessful capture attempts. The following study was designed to examine whether or not largemouth bass would demonstrate selection for size of prey within a single prey species when both soft and spiny-rayed prey were available.

Methods

Subjects

The predators were the same as those used in Experiment II. Bluegill and grass carp were utilized as prey

species. All fish were housed and maintained as in the previous studies. Between the testing of grass carp and bluegill, one predator died and one began to refuse to eat bluegill, despite four weeks of deprivation.

Procedure

Four different sized prey were presented simultaneously to the predators each day. For the grass carp, the size classes varied by 10 mm with four consecutive size classes being presented simultaneously. Smaller size class intervals (5 mm) were employed for the bluegill, due to the smaller range of sizes available before the mouth width of the smaller predators was exceeded by the body depth of the prey. The carp ranged in size from 30 to 110 mm in standard length (SL) as measured from the tip of the snout to the end of the vertebral column. Two presentations of each of the possible combinations of four consecutive size classes were made for each predator. All of the carp were presented before presentations of bluegill began. The same format of presentation was followed for bluegill in the size range from 30 to 75 mm SL.

This method of presentation was employed, rather than having prey continuously available to the bass, because three of the bass in the 68-liter aquaria consistently killed all of the fish with them in the tanks, regardless of the number. The killing was accomplished by continual harassment of the prey in the form of chasing, ramming, and by taking them into the mouth and rejecting at an aver-

age rate of one attack every 30 seconds until all of the fish were dead. One of the bass engaged in this behavior with such vigor that it went ventral up with apparent exhaustion and had to be removed to allow for recovery.

The size of the first fish captured by the bass was recorded whereupon the remainder of the prey were removed from the testing area. This was done to maintain the bass at a sufficient level of deprivation to allow for daily testing.

Results and Discussion

A Chi Square test for goodness of fit was performed on the data (Freund, 1967). There was no evidence of size selection by any of the predators for either of the prey species ($p > .05$ ^{2} values are reported in Appendix 1). There was a significant effect for size of prey on each presentation ($p < .05$) with selection being away from the smaller of the four fish presented, regardless of the size of the smallest fish. There was no effect for the remaining three positions in the presentations. The selection data are presented in Tables 13 and 14, and it appeared that proximity of the prey to the predator and the behavior of the prey determined which prey were selected. However, the three-dimensional nature of relative position between predator and prey made it difficult to establish in all cases which fish was closest to the predator. Rarely did the predator pass one fish to take another unless the fish passed was motionless. Once the predator initiated an

TABLE 13

Size selection for grass carp. The number represents the number of fish selected by the predator in that size class.

		Size class of grass carp								
		30mm	40mm	50mm	60mm	70mm	80mm	90mm	100mm	110mm
	1		1	2	1	4	2	2		
	2		1	1	5	2	2	1		
	3			2	3	2	3	1	1	
	4		1	2	3	4	1	1		
	5			1	4	1	2	2	2	
Bass	6			1	3	4	1	2	1	
	7		1	2	1	2	3	1	1	1
	8		1	2	2	2	3		1	1
	9	1		1	3	2	2	2		1
	10	1		1	3	2	2			1

TABLE 14

Size selection for bluegill. The number represents the number of fish selected by the predator in that size class.

		Size class of bluegill									
		30mm	35mm	40mm	45mm	50mm	55mm	60mm	65mm	70mm	75mm
	1	1	1		2	2	2	2	1		
	2			3	3	2	2	2	2		
	3		1	1	2	4	1	3	2		
	4		1	2	2	1	1	5	1	1	
	5		1	2	1	1	3	4	1		1
Bass	6			3	3		2	2	1	3	
	7		1	2	2	2	1	2	2	1	1
	8	1		2	2	2	2	3	1		1

attack on one prey rarely did it deviate to other prey even when the attack resulted in an extended chase sequence.

INCIDENTAL OBSERVATIONS

A number of observations were made during the course of these studies that were not systematically recorded, yet were none the less interesting and informative.

Regurgitations of swallowed prey were very common if the bass were disturbed, as often happened when the remaining prey were removed during tests for size selection. The fish was expelled by a series of stomach contractions and yawns. Regurgitations of partially digested fish were also common if the fish was guite large. This became apparent when tests were made to determine whether the largest size of grass carp available to the predator was a function of length or depth of body. The length of a grass carp may approach 60% of the length of the predator before depth of body becomes a limiting factor. In contrast, a bluegill, 30 percent of the length of the bass may exceed the gape width in body depth.

In most cases, it was necessary to deprive the bass for a minimum of three days before they would accept grass carp between 45 and 60% of the body length of the bass. Usually in such cases, the tail and a portion of the caudal peduncle protruded from the mouth of the bass for up to two hours. Typically, such fish were found partially digested and regurgitated on the bottom of the tank the

following day.

Bluegill that had been chased or lunged at repeatedly by the predator and were motionless on the sides of the tank, often with their heads oriented upward, downward, or horizontally, could be picked up out of the water in the observer's hand. It was also noted that such fish, with their heads oriented upward, would occasionally begin to roll backward with the ventral up. The fish usually regained its original posture before it had rolled completely over.

Occasionally a fish apparently would be tonically immobile when introduced into the tank. That is, except for the gills, the fish would be completely immobile, with the pectoral fins directed outward from the body. The fish spontaneously began swimming after a variable length of time if not disturbed by the predator. The predator's response to the fish was the same as that to any motionless fish with the occasional exception that occurred if the predator approached and yawned at the prey. If the prey did not respond to the yawn the predator turned away. However, in most cases the immobile fish responded with escape swimming.

With very large prey, such as bluegill near the limits of the bass' mouth, the predator expended considerable effort apparently attempting to position itself in front of the prey. In chases, the predator would swim up alongside of the prey, or past the prey, forcing the prey to turn.

There were very few attempted captures of very large prey that would result in the prey being taken into the mouth tail first.

GENERAL DISCUSSION

In this study, differences in the susceptibility of the different species to predation by largemouth bass have been demonstrated. Further, the manner in which the predator interacts with the prey varies across species. Risk to the prey was found to be consistently related to movement of the prey in the vicinity of the predator. Inhibition of movement decreased risk, while movement, particularly rapid movement, resulted in a substantial increase in risk. To some extent, the movement of the prey was induced by the behavior of the predator, especially yawning behavior. Those prey which did not respond to the behavior of the predator enjoyed a lower risk to predation.

The field literature on the feeding behavior of largemouth bass indicates movement to be a significant variable. (McClane, 1955; Kramer and Smith, 1960; Chew, 1974). Moehn (1959), examined the hypothesis that the high incidence of empty stomachs observed in field-collected largemouth bass is due to the low vulnerability of the forage species. He found that rotenone poison, lightly applied to the surface of a small lake, reduced the incidence of empty stomachs significantly and increased the number of items per stomach. The bass appeared to be gorging themselves on the dying fish. Rotenone, while ultimately asphyxiating the fish, causes very erratic swimming by the fish. Since the

smaller fish are affected before the larger fish, the erratic swimming behavior of the small fish is generally regarded as the stimulus condition eliciting a feeding frenzy (Zweiacker and Summerfelt, 1973; Moehn, 1959; Lewis et al., 1974) in the bass. The implication from this research is that the forage fish have low vulnerability to bass predation under normal conditions. In all probability, the low vulnerability of the prey species is related to both movement patterns on the part of the prey and the utilization of cover.

The propensity of the bass to capture fish that were moving could be due to several factors. First, motionless prey are less conspicuous in their environment than are moving prey. Several times the bass apparently ignored motionless prey but immediately responded to the same fish when it moved. It should be added here that many of the orientations to motionless prey, in this study, were to prey to which the predator had previously oriented when introduced, thus the predator might have known their location.

Second, the apparent tendency to take moving prey may simply have been the result of the prey responding with movement to an approaching predator. A third possibility is that the predator actively induced movement on the part of the prey. Yawning was very effective in this respect. Yawning was usually directed at motionless prey close to the sides of the tank, with the notable exception of the

behavior toward immobile prey. The yawning behavior of the bass probably counteracts, to some extent, the utilization of cover by the forage species. Obviously, a predator cannot lunge at a prey if the prey is near cover that will physically obstruct the lunge. Yawning could cause the prey to move away from the cover, thus affording the bass an opportunity to capture the prey.

A final possibility is that the bass responds to sudden and rapid movement in its vicinity with orientation and rapid approach. If it is going to enjoy success, a predator, such as bass, that preys upon highly mobile prey, should respond to sudden movements in its environment with approach. Hesitation may permit the escape of the prey. It was noted during the course of the study that prey swimming at escape speed almost always precipitated a chase by the bass whether or not the bass had been oriented toward the prey when the swimming was initiated and regardless of whether or not the bass had just turned away from the prey. This kind of responsiveness to sudden movement by the bass may be the basis for the reflexive feeding reported for piscivorous predators (Hobson, 1968; Lewis et al., 1974). In any event, it is probable that the high risk to moving prey is a result of a combination of all of these factors, although further research could do much to clarify the issue.

Lewis (Lewis, Gunning, Lyles and Bridges, 1961; Lewis, Anthony, and Helms, 1964; Lewis, 1967; Lewis, Heidinger,

Kirk, Chapman, and Johnson, 1974) contends that bluegill have very low vulnerability to largemouth bass predation relative to other species of prey. The data obtained in this study also indicate that bluegill have a lower risk to bass predation.

The relatively low risk of the bluegill, as measured by sequence length and capture/success ratios, appears to be primarily due to the movement pattern of the bluegill, including responsiveness to the predator and utilization of cover; but is probably also due to the relative depth of body and the presence of spiny-rays. The presence of spines in the fin ray of both bluegill and bass fingerlings increased the difficulty that the predator encountered in swallowing these species. While there were no obviously different handling or capture techniques employed by the bass to capture spiny-rayed prey, it is interesting to note that most of the spiny-rayed captures resulted in the prey being taken into the mouth tailfirst. Since mode of capture determines the position of the fish in the mouth, and mode of capture is an interactive effect of the behavior of both the predator and the prey, it may be that the spiny-rayed prey were maintaining a position, relative to the predator which dictated a tailfirst capture, and which, in turn, resulted in significantly more rejections of the prey, and hence, more opportunities for the prey to escape.

The relationship between depth of body and weight suggest that the bluegill is not an optimal configuration for

predation by largemouth bass. Lawrence's (1960) data indicate that at the limit of gape width for bass in the 12 inch class, acceptable bluegill weight a third of what a bass would weigh and slightly more than half of what a golden shiner would weigh. Although he did not include grass carp in his equations, the relationship in weight at maximum depth for the two species is with the bluegill being the lighter of the two species. Coupled with the difficulty the bass encounters in capturing and swallowing bluegill, the weight considerations suggest the bass should utilize an alternative source of prey, if available.

Equation for body depth, above and below 0.59, the gape width of the predator, resulted in more uniformity in sequence length for the larger prey across all species except the grass carp. Moreover, it revealed a positive relationship between sequence length and body depth for all species, again excepting grass carp. The disparity in sequence length between large and small prey appeared to be due, primarily, to a greater number of unsuccessful attempted captures of larger prey along with a greater number of behaviors designed to place the predator in a position to capture the prey.

Doubtless there is a point at which the difficulty encountered by the bass in capturing larger prey exceeds the additional energy value provided by the larger prey. However, observations of the bass when presented with multiple prey

suggests the possibility that the bass may be basically opportunistic across the range of prey sizes that it is capable of swallowing. If such is the case, prey size in the diet may be determined by the conspicuousness of the prey, with smaller prey being less conspicuous, than larger prey at equivalent distances from the predator, while more of the larger prey would escape attempted captures by the bass.

There did not appear to be a consistent relationship between depth of body and difficulty in swallowing. This finding is surprising since it would be expected that the larger fish, by virtue of being nearer the physical capacity of the predator, would result in greater difficulty in swallowing. It would seem that there is some other factor, beside the presence of spines and depth of body, responsible for the difficulty experienced by bass in swallowing bluegill. This suspicion is reinforced by the fact that despined bluegill caused as much difficulty as intact bass of equivalent size.

Grass carp neither avoided nor escaped predation with any degree of success. In observing this species it did not appear that the grass carp modified their swimming behavior in the presence of the predator, although they were responsive to behaviors by the bass that were directed toward them. The lack of inhibition of movement, the absence of spiny-rays and the body configuration of the grass carp combine to suggest that this species would be highly vulnerable to bass predation in the field.

APPENDIX I

Statistical Summary Tables

TABLE 1-A

Z tests for efficiency of capture between species of prey.

	Shiner	Bluegill	Bass	Carp
Capture	126	102	70	70
Attempt	259	275	184	104

Shiner-Bluegill	Z=2.59*		
Shiner-Bass	Z=2.31*	Bluegill-Bass	Z=0.22
Shiner-Carp	Z=3.10*	Bluegill-Carp	Z=5.26*

Bass-Carp Z=4.75*

*Significant at the p = .05 level or greater.

TABLE 2-A

Z tests for proportion of captures to frequency of normal and escape swimming between species of prey.

	Shiner	Bluegill	Bass	Carp
Capture	85	83	81	62
Normal/escape	264	345	130	131

Shiner-Bluegill	Z=2.16*		
Shiner-Bass	Z=5.66*	Bluegill-Bass	Z=7.76*
Shiner-Carp	Z=2.94*	Bluegill-Carp	Z=4.89*

Bass-Carp Z=2.42*

*Significant at the p = .05 level or greater.

TABLE 3-A

Z tests for the proportion of motionless and pectoral responses to all swimming responses between species of prey.

	Shiner	Bluegill	Bass	Carp
Motionless	235	507	85	79
Total Responses	499	852	215	208

Shiner-Bluegill	Z=4.64*		
Shiner-Bass	Z=1.75	Bluegill-Bass	Z=5.26*
Shiner-Carp	Z=2.50*	Bluegill-Carp	Z=6.05*

Bass-Carp Z=0.64

*Significant at the p = .05 level or greater.

TABLE 4-A

Z-tests for proportion of captures to frequency of motionless responses between species.

	Shiner	Bluegill	Bass	Carp
Capture	18	19	2	3
Motionless	140	323	76	55

Shiner-Bluegill	Z=2.59*		
Shiner-Bass	Z=2.50*	Bluegill-Bass	Z=1.07
Shiner-Carp	Z=1.90	Bluegill-Carp	Z=0.57

Bass-Carp Z=0.59

*Significant at p = .05 level or greater.

TABLE 5-A

Z tests for proportion of responses by the prey to approaches by the predator.

	Shiner	Bluegill	Bass	Carp
Responses	41	106	45	22
Approaches	349	469	81	46

Shiner-Bluegill	Z=4.07*		
Shiner-Bass	Z=10.23*	Bluegill-Bass	Z=6.42*
Shiner-Carp	Z= 6.85*	Bluegill-Carp	Z=3.88*

Bass-Carp Z=0.78

*Significant at p = .05 level or greater.

TABLE 6-A

Z tests for proportion of headfirst captures to tailfirst and sideways captures following intercept.

	Shiner	Bluegill	Bass	Carp
Headfirst	16	16	13	27
Total captures	18	19	15	38

Shiner-Bluegill	Z=0.42		
Shiner-Bass	Z=0.18	Bluegill-Bass	Z=0.24
Shiner-Carp	Z=1.50	Bluegill-Carp	Z=1.07

Bass-Carp Z=1.23

TABLE 7-A

Z tests for proportion of tailfirst captures to headfirst and sideways captures following chase.

	Shiner	Bluegill	Bass	Carp
Tailfirst	19	32	43	28
Total captures	33	39	43	29

Shiner-Bluegill Z=2.24*
Shiner-Bass Z=4.72
Shiner-Carp Z=3.58

Bluegill-Bass Z=2.86*
Bluegill-Carp Z=1.89

Bass-Carp Z=1.40

*Significant at p = .05 level or greater.

TABLE 8-A

Z tests for proportion of headfirst captures to tailfirst and sideways captures following a lunge.

	Shiner	Bluegill	Bass	Carp
Headfirst	50	15	1	1
Total Captures	75	44	14	15

Shiner-Bluegill Z = 3.67*
Shiner-Bass Z = 4.16*
Shiner-Carp Z = 2.90*

Bluegill-Bass Z=1.97*
Bluegill-Carp Z=0.50

Bass-Carp Z=1.43

*Significant at p = .05 level or greater.

TABLE 9-A

Z tests for proportion of yawns occurring before capture to captures.

	Shiner	Bluegill	Bass	Carp
Yawns	64	98	10	2
Captures	127	107	70	81

Shiner-Bluegill Z=6.83*
Shiner-Bass Z=5.00*
Shiner-Carp Z=7.27*

Bluegill-Bass Z=10.41*
Bluegill=Carp Z=12.19*

Bass-Carp Z=2.73*

*Significant at p = .05 level or greater.

TABLE-10A

Z tests for the combined proportion of gill flares, headshakes, and yawns after capture to the number of captures.

	Shiners	Bluegill	Bass	Carp
Difficulty	11	123	42	12
Captures	127	107	70	81

Shiner-Bluegill	Z=16.56*		
Shiner-Bass	Z= 7.73*	Bluegill-Bass	Z=14.10*
Shiner-Carp	Z= 1.36	Bluegill-Carp	Z=15.38*

Bass-Carp Z=5.77*

*Significant at p = .05 level or greater.

TABLE-11A

Z tests for proportion of rejects to captures between species.

	Shiners	Bluegill	Bass	Carp
Rejects	15	24	3	1
Captures	127	107	70	81

Shiner-Bluegill	Z=2.04*		
Shiner-Bass	Z=1.90	Bluegill-Bass	Z=3.27*
Shiner-Carp	Z=2.89*	Bluegill-Carp	Z=4.12*

Bass-Carp Z=1.07

*Significant at p = .05 level or greater.

TABLE 12-A

Z tests for differences between shiners above and below 0.59 the gape width of the predator involved.

		Above 0.59	Below 0.59	Z Value
Effic.	Capture Attempt	36 121	80 138	4.51*
Intercept	Capture Attempt	7 17	11 15	1.45
Lunge	Capture Attempt	17 48	58 79	4.27*
Chase	Capture Attempt	12 56	21 44	2.84*
Diff.	Gill Flare Capture	3 36	5 91	0.64
Diff.	Yawn Capture	2 36	0 91	-
Diff.	Headshake Capture	0 36	1 91	-
Rejects	Rejects Capture	11 36	4 91	4.22*
Risk	Captures Motionless	1 109	17 31	7.94*
Risk	Captures Normal	17 68	36 74	2.93*
Risk	Captures Pectoral	9 54	15 41	2.25*
Risk	Captures Escape	9 67	23 55	3.63*
Response Pattern	Motionless Total response	109 298	31 201	4.89*
Response Pattern	Normal Total response	68 298	74 201	3.50*
Response Pattern	Pectoral Total response	54 298	41 201	0.56
Response Pattern	Escape Total response	67 298	55 201	1.39

TABLE 13-A

Z tests for differences between bluegill above and below 0.59 the gape width of the predator involved.

		Above 0.59	Below 0.59	Z Value
Effic.	Capture Attempt	77 215	24 60	0.57
Intercept	Capture Attempt	14 16	5 5	0.78
Lunge	Capture Attempt	34 88	10 28	0.32
Chase	Capture Attempt	29 111	10 27	1.15
Diff.	Gill flare Capture	32 77	10 36	1.43
Diff.	Yawn/after Capture	38 77	6 36	3.24*
Diff.	Headshake Capture	28 77	7 36	1.82
Rejects	Rejects Capture	17 77	7 36	0.37
Risk	Captures Motionless	14 281	5 42	1.79
Risk	Captures Normal	30 163	9 13	4.25*
Risk	Captures Pectoral	5 162	0 22	-
Risk	Captures Escape	32 146	12 23	3.09*
Mode of capture	Intercept Attempts	16 215	5 60	0.25
Mode of capture	Lunge Attempts	88 215	28 60	0.69
Mode of capture	Chase Attempts	111 215	27 60	0.82
Position in mouth	Headfirst Captures	30 77	6 24	1.24

TABLE -13A (continued)

		Above 0.59	Below 0.59	Z Values
Position in mouth	Tailfirst Captures	42 77	17 24	1.98*
Position in mouth	Sideways Captures	5 77	1 24	0.36
Predator Position	Yawns/before Captures	92 77	6 36	16.45*
Predator position	Approach Total	420 2174	38 320	3.04*
Predator position	Stop Total	417 2174	32 320	3.91*
Predator position	Follow Total	72 2174	3 320	2.40*

TABLE 14-A

Z tests for differences between bass above and below 0.59 the gape width of the predator involved.

		Above 0.59	Below 0.59	Z Value
Effic.	Capture Attempt	13 69	57 115	4.25*
Intercept	Capture Attempt	3 5	10 10	2.17*
Lunge	Capture Attempt	1 21	13 45	2.23*
Chase	Capture Attempt	9 43	34 60	3.71*
Diff.	Gill Flare Captures	2 15	15 68	0.79
Diff.	Yawn/after Captures	1 15	12 68	0.87
Diff.	Headshake Capture	0 15	12 68	-
Rejects	Rejects Captures	1 15	2 68	0.71
Risk	Captures Motionless	0 19	2 57	-
Risk	Captures Normal	6 16	25 43	1.37
Risk	Captures Pectoral	0 4	0 5	-
Risk	Captures Escape	9 20	41 51	2.91*
Predator position	Yawns/before Captures	8 15	2 68	5.38*
Predator position	Approach Total	39 271	42 471	2.08*
Predator position	Stop Total	45 271	12 471	7.00*
Predator position	Follow Total	4 271	2 471	1.39

TABLE 14-A (continued)

		Above 0.59	Below 0.59	Z Value
Mode of capture	Intercept Attempts	5 69	10 115	0.49
Mode of capture	Lunge Attempts	21 69	45 115	1.29
Mode of capture	Chase Attempts	43 69	60 115	1.39
Position in mouth	Headfirst Captures	3 13	10 57	0.50
Position in mouth	Tailfirst captures	10 13	47 57	0.50

TABLE 15-A

Z tests for differences between spined and de-spined bluegill.

		Spined	De-spined	Z Values
Diff.	Gill Flares Captures	42 96	15 82	3.28*
Diff.	Yawn/after Captures	46 96	9 82	5.29*
Diff.	Headshakes Captures	35 96	13 82	2.99*
Rejects	Rejects Captures	15 96	11 82	0.56
Position in mouth	Headfirst Captures	37 96	48 82	2.67*
Position in mouth	Tailfirst Captures	59 96	34 82	2.67*
Mode of Capture	Intercept Attempt	21 275	21 82	4.00*
Mode of Capture	Lunge Attempt	116 275	50 82	3.02*
Mode of Capture	Chase Attempt	138 275	21 82	3.87*

TABLE 16-A

Z tests for differences in the proportion of gill flares, headshakes, yawns, and rejections as a function of position of the prey in the mouth of the predator for both spined and de-spined bluegill.

		Gill flare		Yawn		Headshake		Reject	
		Head	Tail	Head	Tail	Head	Tail	Head	Tail
Spined	Responses	22	20	18	28	7	28	1	14
	Capture	37	59	37	59	37	59	37	59
	Z Value	2.40*		0.19		2.80*		2.73*	
De-spined	Responses	8	7	5	4	2	11	7	4
	Capture	48	34	48	34	48	34	48	34
	Z Value	0.47		0.23		3.41*		0.40	

TABLE 17-A

Chi square tests of goodness of fit on size selection data from grass carp and bluegill.

Fish number	X^2 Value	DF	Significance
	Grass Carp		
1	5.50	6	.05
2	7.50	6	.05
3	5.00	6	.05
4	7.00	6	.05
5	7.00	6	.05
6	7.00	6	.05
7	4.00	6	.05
8	4.00	6	.05
9	5.00	6	.05
10	3.00	6	.05
	Bluegill		
1	8.50	7	.05
2	5.17	7	.05
3	4.34	7	.05
4	6.84	7	.05
5	-	-	-
6	4.84	7	.05
7	8.17	7	.05
8	-	-	-
9	1.84	7	.05
10	3.84	7	.05

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BIOGRAPHICAL SKETCH

Daniel C. Hatton was born in Aberdeen, Washington on March 4, 1944. In May, 1961 he was graduated from Moclips-Aloha High School in Moclips, Washington. In April, 1967 he joined the United States Air Force. After serving four years in the Air Force, he enrolled at Grays Harbor Community College in Aberdeen, Washington where he met and married the former Nikki Chapin of Stevenson, Washington. In June of 1969 he received an associate of Arts degree from Grays Harbor College. The follwing September he enrolled at the University of Washington in Seattle, Washington where he received his Bachelor of Arts in Psychology in March of 1971. In September of 1971 he began work as a graduate student at Western Washington State College in Bellingham, Washington. He was graduated with a Master of Science in Psychology from Western Washington in August of 1972. He began work as a graduate student at the University of Florida in September, 1972, and is presently a candidate for the degree of Doctor of Philosophy at the University of Florida.

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

Merle E. Meyer, Chairman
Professor of Psychology

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

Donald A. Dewsbury
Professor of Psychology

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

Robert L. Isaacson
Professor of Psychology

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

Edward F. Malagodi
Associate Professor of Psychology

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

Thomas H. Patton

Thomas H. Patton
Associate Curator of Natural Sciences
Florida State Museum

This dissertation was submitted to the Graduate Faculty of the Department of Psychology in the College of Arts and Sciences and to the Graduate Council, and was accepted as partial fulfillment of the requirements for the degree of Doctor of Philosophy.

March, 1977

Dean, Graduate School